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A NEW ANTHRACOSAURIAN LABYRINTHODONT, *PROTEROGYRINUS SCHEELEI*, FROM THE LOWER CARBONIFEROUS

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ABSTRACT

Incomplete remains of the skull and skeleton of an anthracosaurian labyrinthodont from the basal part of the Mauch Chunk Group of the Mississippian of Greer, West Virginia, are described as *Proterogyrinus scheelei*, gen. et sp. nov. and made the type of a new family Proterogyrinidae. The type resembles the Embolomeri in most regards but is more primitive in that both intercentra and pleurocentra are in the form of dorsally incomplete rings.

INTRODUCTION

As noted in a previous publication in this series (Romer, 1969), almost nothing has been known of labyrinthodont amphibians in the earlier, Mississippian, portion of the Carboniferous. This lacuna is in process of being filled in considerable measure by specimens from the Greer quarry in West Virginia. In my previous paper I noted the history and stratigraphy of the locality. In that paper I described the skull and partial skeleton of a rhachitome from Greer; specimens of an anthracosaur and a second rhachitome are in process of description by Dr. Nicholas Hotton III; several further Greer specimens are in process of study and collection. It is to be hoped that before the possibilities of the Greer quarry are exhausted we may attain a broad representation of the labyrinthodont fauna of the Lower Carboniferous of North America.

Science is indebted to Mr. John J. Burke and Mr. William E. Moran and, more recently, to Mr. William Hlavin for their success-

ful exploration of the Greer site, to the Greer Limestone Company, owners of the property, for their cooperation, and to Mr. William E. Scheele, Director of the Cleveland Museum of Natural History, for his promotion of the work.

In the present paper is described an anthracosaur differing from that under description by Dr. Hotton. The specimen is fragmentary in nature, but is of interest, particularly, as showing a hitherto unknown type of anthracosaurian vertebral structure.

SYSTEMATIC PALEONTOLOGY

Family PROTEROGYRINIDAE fam. nov.

Diagnosis: Anthracosaurian labyrinthodonts, resembling typical embolomeres in most regards, but with both intercentra and pleurocentra in the form of incomplete rings, open dorsally. Type genus *Proterogyrinus.*

Genus **Proterogyrinus**[1] gen. nov.
Proterogyrinus scheelei[2] sp. nov.
Figs. 1-8

Diagnosis for genus and species: Structure, so far as known, similar in most regards to such an embolomere as *Archeria.* Snout moderately elongate; length of frontal and nasal combined nearly twice as long as parietal and postparietal. Skull roof lightly sculptured with small shallow pits and short grooves.

Holotype: Cleveland Museum of Natural History 10950.

Occurrence: Bickett Shale of the Bluefield Formation, Mauch Chunk Group, Mississippian.

Locality: Greer, Monongalia County, West Virginia, on Deckers Creek, about 6½ miles southeast of Morgantown.

Repository: Cleveland Museum of Natural History, Cleveland, Ohio.

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[1] The generic name continues the series of anthracosaurian names based on "gyrinus" by Watson, and suggests the relative antiquity of the present form.

[2] The specific name is in honor of Director William E. Scheele, who has enthusiastically promoted the search for Greer amphibians.

DESCRIPTION

Cranial remains: Two large slabs show disarticulated and scattered postcranial remains; a smaller block contains incomplete remains of cranial structures (as well as several anterior vertebrae) (Figs. 1-2).

Best preserved of skull materials are the dorsal series of roofing bones, from nasals back to postparietals and tabulars. These are preserved almost intact except for some disruption of the right side of the table posteriorly. This type of preservation of the skull roof is common in anthracosaurs, due principally to the loose connection of skull table and cheek in typical members of this group, and aided anteriorly by the apparently sharp drop of the sides of the snout from the frontals and nasals. For example, in the Harvard collection of *Archeria* materials from the Geraldine bonebed of the Texas Permian, no less than five specimens show a complete or nearly complete series of dorsal roofing elements broken off from the elements of the side of the skull. The skull roof is but lightly sculptured; near centers of ossification there are groups of small, shallow pits; farther out one finds a series of short and shallow radiating grooves. Of lateral line grooves, only faint and uncertain traces are to be seen.

The skull table structures are comparable to those of embolomeres. Slender tabular "horns" are present, although broken off. In the lateral series of table elements, the tabulars are somewhat larger than typical, and in consequence the two temporal elements are somewhat reduced in size. The suture between intertemporal and supratemporal is obscure, but apparently the former element is of small size. The parietal does not expand as much posterolaterally as is usually the case.

Facial length is variable in anthracosaurians, but snout elongation is common in embolomeres. If we assume that the joint length of parietals plus postparietals is relatively constant, we find that, for example, the length of nasals and frontals together is about 180 percent of this figure in *Palaeogyrinus*, 260 percent or so in members of the *Pteroplax-Eogyrinus* group, 300 percent and upward in *Archeria*. *Proterogyrinus* is relatively short faced, with nasal and frontal about twice the length of the posterior table elements.

Apart from the dorsal roofing elements, skull remains are few and generally scattered. Fragments of both prefrontals and of the

Fig. 1. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. The block exhibiting cranial materials, × ¾.

left postorbital are seen adjacent to the dorsal series. Far to the right of the skull table is a roughly triangular mass of bone which may represent the right cheek area of squamosal and quadratojugal. Several other pieces of bone lying to the right of the skull roof may be part of the dermal elements of the right side of the face, but I have not attempted to identify them.

To the right is found a crushed but nearly complete right pterygoid, seen from the inner or lower surface; in its extent it is comparable to that of *Palaeogyrinus* as figured by Watson (1926) and by Panchen (1964). The thickened portion of the epipterygoid supporting the anteroventral surface of the basipterygoid process is evident, but the more dorsal region of the socket for the process is not clear. A bar of bone rising straight upward from this area is presumably an imperfect columella cranii; whether further remains

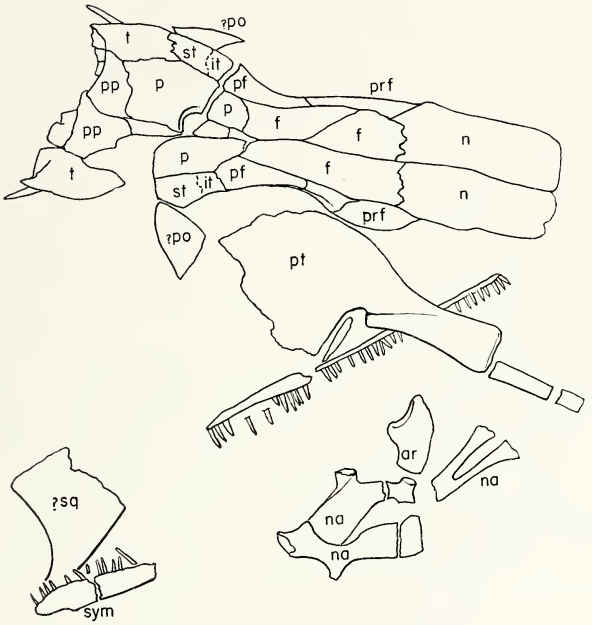

Fig. 2. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. To show, in outline, identified elements present on the block shown in figure 1, × ¾: *ar,* articular region of right lower jaw; *f,* frontal; *it,* intertemporal; *n,* nasal; *na,* neural arch; *p,* parietal; *pf,* postfrontal; *po,* postorbital; *pp,* postparietal; *prf,* prefrontal; *pt,* pterygoid; *sq,* squamosal; *st,* supratemporal; *sym,* symphysial region of right lower jaw; *t,* tabular.

of the epipterygoid are present, concealed beneath the pterygoid, cannot be determined.

A bar of bone bearing about 40 teeth (plus a few empty alveoli) is seen to the right of the series of dorsal elements.[1] The tooth row is of length appropriate to its being considered nearly a full dentition for a maxilla or dentary of the present specimen. Most of the teeth are about 3 mm long, subcircular in section, about ¾ mm in diameter and closely spaced. In some cases the basal section of the tooth can be seen to be grooved in labyrinthine fashion. The tips are blunt and when well preserved appear to be bevelled and tilted slightly toward that end of the bar which lies anteriorly on the slab.

[1] A section of this series running beneath the pterygoid has been developed since the photograph of figure 1 was taken.

The nature of this tooth-bearing element is somewhat puzzling. At first sight one would assume that it is the right maxilla, little displaced. But there is a distinct longitudinal shelf the length of the bone, superficial to the teeth as they lie on the bone. We are, hence, looking at the inner surface of the bone. But if the bone is a maxilla, it must be either the left element strongly displaced, or the right maxilla rotated nearly 180°. Suggesting the latter interpretation is the fact that the teeth which lie most anteriorly are smaller than most of the series, and hence may pertain to the posterior end of the tooth series.

To add complexity to the situation, there are present, further to the right in the slab and not far from the "front" end of the tooth-bearing element, the articular end of a right lower jaw and, far to the rear, the symphysial end of a right jaw. It is tempting to consider that the major structure we are dealing with is a dentary, rather than a maxilla. However, to make it a right dentary requires not only that the smaller teeth be considered anterior, but necessitates such a complex post-mortem juggling of parts that it seems

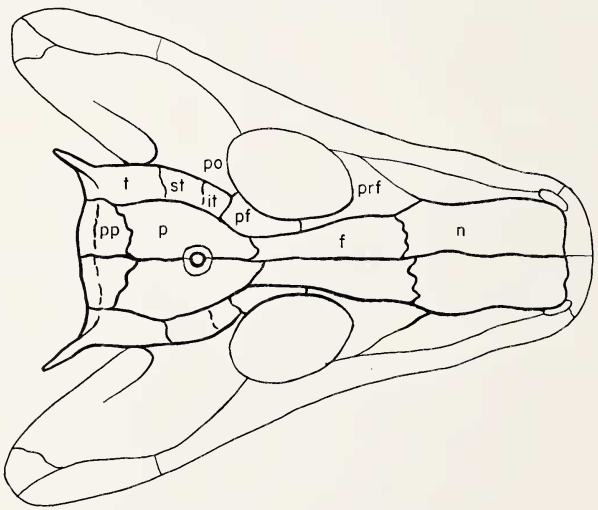

Fig. 3. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Attempted restoration of skull in dorsal view. Heavy lines indicate parts preserved in the specimen; light lines, lateral portions of skull restored in embolomere pattern. Abbreviations as in fig. 2, × ¾.

better to keep to the assumption that we are dealing with a displaced right maxilla.

Assuming normal proportions and arrangement of the dermal roofing elements as found in other anthracosaurs, one can tentatively restore the appearance of the skull as seen in dorsal view (fig. 3). Material is obviously insufficient for an attempt at a lateral or ventral reconstruction.

POSTCRANIAL SKELETON

Axial skeleton: From the small block containing the remains of the skull, disarticulated postcranial materials are sparsely spread over two slabs extending for about 70 cm. Except for a partial *Megalichthys* jaw near the far end of the slabs, all material visible is of a sort which could have been derived, and presumably did derive, from a single animal. All identifiable materials are appropriate to a form with body and limb proportions similar to those of the embolomere *Archeria,* and in various points the structure of limb and girdle remains are comparable to those of typical embolomeres. Despite their disarticulated and scattered nature, the various preserved fragments indicate that the individual had not completely "disintegrated" before burial; for example, the remains of the front leg are close to the skull block, remains of the pelvic girdle are toward the far end of the pair of slabs.

There are sparse scattered remains of the vertebral column. Several neural arches, presumably from the cervical region, are present on the skull slab. About a dozen arches from the trunk region can be seen; on the larger slabs most are crushed or incomplete, and surface detail is generally obscure. However, the general structure can be made out (fig. 4 D,E). It is of a normal anthracosaurian type. The neural spine is moderately tall, thin from side to side, and broad anteroposteriorly. Below, the arch expands anteriorly and posteriorly to the zygapophyses; further ventrally and somewhat anteriorly the arch extends downward to, presumably, afford tubercular attachment for the rib externally, and internally shows a flat surface for "central" attachment.

Separated from the arches there are found some eight "central" elements (fig. 5). They are thin hoops of bone, forming the greater part of a circle but incomplete at one point, presumably dorsally

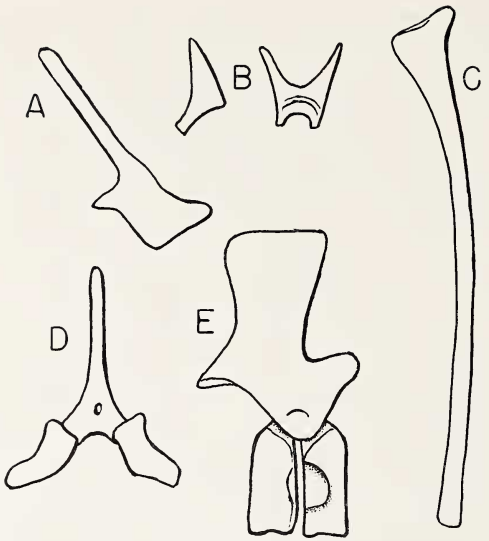

Fig. 4. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. *A,* a caudal neural arch, seen from the right side. *B,* a caudal intercentrum and haemal arch base, seen from the side at the left, anteroventrally at the right. *C,* a rib; position in column indeterminate. *D,* a dorsal neural arch in anterior view. *E,* a dorsal neural arch in side view; central elements are restored in probable position, × 3/2.

in the articulated position. The upper edges are bevelled, obviously for neural arch articulation. Most of these central elements are poorly preserved, but several, when seen in side view, have nearly straight edges, with little indication of structural features except for a slight indentation seen in two cases part way down the presumed anterior border. One element, however, is of a different nature, and a second element appears to resemble it. Here, part way down each side, there is a pronounced development of a semicircular area of articulation for a rib capitulum along the presumed

Fig. 5. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. "Central" elements of the trunk. *A,* presumed intercentrum from the right side and posteriorly. *B,* presumed pleurocentrum from the right side and posteriorly, × 3/2.

posterior margin of the outer surface. It seems probable that we have in these ring-shaped structures both pleurocentra and intercentra, those with the pronounced articular area being intercentra, the others pleurocentra. I have ventured to restore a vertebra in side view (fig. 4 E). This restoration should, of course, be considered as tentative only, because of the sparsity and disarticulated condition of the material. As seen in side view, the vertebra appears closely comparable to that of a typical embolomere. It must be remembered, however, that the central elements are merely thin shells, in strong contrast to the centra of such a typical embolomere as *Archeria* and, further, that the "central" rings, as preserved, are incomplete dorsally. It is not impossible that in a more mature specimen of *Proterogyrinus* this dorsal gap might have been closed; but it is highly improbable that, even so, the elements would have been closely comparable to those of typical embolomeres, in which ossification is as complete dorsally as around the rest of the circle of the centrum. Of the caudal region I have been able to identify a single neural arch, of relatively small size and with a slender backwardly-slanting spine (fig. 4 A). Adjacent to one of the ischia there are badly preserved remains of the central elements of a fraction of the tail region. There are here several intercentral elements, from which the haemal spines have broken off (fig. 4 B). The associated intercentra appear, as far as preserved, to be wedge-shaped, as seen in side view, tapering to a point dorsally. A crushed and poorly preserved element nearby appears to be a completely circular structure. Possibly pleurocentral development may have been more advanced in the caudal region than in the trunk.

In the neighborhood of the front limb are remains of two clusters of ribs which presumably come from the anterior part of the column. The rib heads are not visible. They are circular in section, and show none of the flattening seen in various temnospondyls, and there is no evidence of expansion of the shaft (except for a slight distal expansion seen in one case). A few further ribs are seen farther posteriorly in the block; one is shown in figure 4 C.

There are a number of belly scales, poorly preserved, scattered over the slabs.

Appendicular skeleton: There are no identifiable remains of the shoulder girdle. Of the left pectoral limb there is only an imperfectly preserved humerus. Of the right leg, however, humerus,

radius and ulna are present close together in a semi-articulated condition (fig. 6 A).

The humerus, which measures 30 mm in overall length, is closely comparable to that of the embolomerous *Archeria* in general build. The bone is less completely ossified than in most specimens

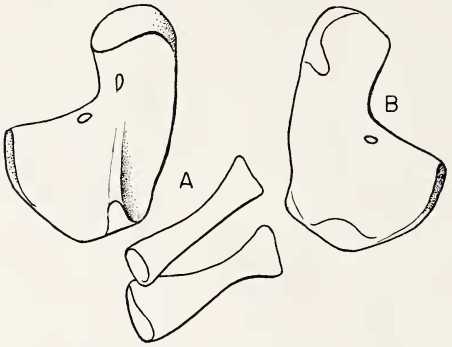

Fig. 6. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. *A,* right humerus; radius and ulna in position as found. The humerus is seen from the dorsal surface. *B,* the same humerus in ventral view, × 1.

of that genus, so that the "unfinished" proximal surface extends anteroventrally to include the region of the deltopectoral crest, and distally the ectepicondyle, presumably projecting in an adult, is unossified. As in *Archeria,* the entepicondyle is a very large subquadrate structure, bearing, as is proper for anthracosaurians, an entepicondylar foramen near its proximal inner corner. As in embolomeres, a highly developed flange of bone extends from the region of the deltopectoral crest distally, without interruption, along the anterior edge of the bone, to the ectepicondylar region.

Radius and ulna are seen from the dorsal (extensor) aspect; the former is 18 mm in length, the latter 20 mm. It is obvious that ossification was far from complete, for in the ulna there is no olecranon and not even any trace of the articular surface for the humerus.

Situated some 60 mm from the major limb bones is a series of disarticulated foot elements which are not improbably part of the right front foot (fig. 7). Presumably, the four stouter elements are metacarpals.

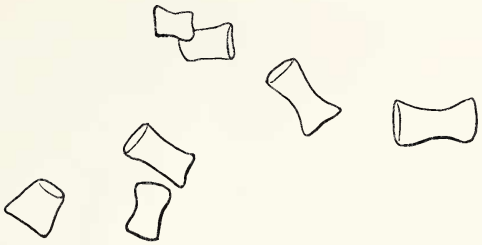

Fig. 7. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Scattered foot bones found near right leg elements, × 1.

Of the pelvic girdle (fig. 8) the left ilium is present, and seen from the inner surface, and there are both ischia, the right seen from the inner surface, the left from the outer side. The greatest length of the ilium, from the pubic articulation to the tip of the posterior prong is 54 mm. The right and left ischia are, respectively, 33 and 32 mm in greatest length. The ilium is closely comparable

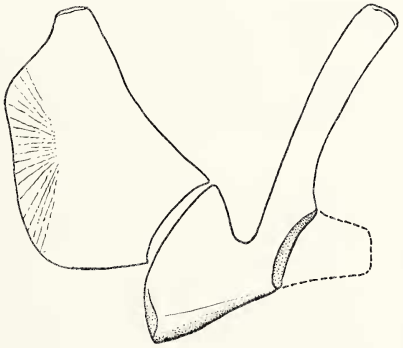

Fig. 8. *Proterogyrinus scheelei* Romer, C.M.N.H. 10950. Left ilium and ischium, seen from inner surface. The ischium is that of the right side, reversed, × 1.

to that of *Archeria*. There obviously was a dorsal blade, for sacral connection, but this is broken off. The posterior prong is as elongate as that of *Archeria*. Since the element is seen from the inner side, nothing can be said of acetabular structure. The base of the bone presents a much thickened articular surface for pubis and ischium, the pubic area being especially thick. Anteriorly there is a well

developed triangular buttress leading down to the region of pubic articulation. This area faces nearly directly anteriorly, in contrast to its somewhat more medial slant in *Archeria.*

The ischium, again, is comparable in proportions and build to that of *Archeria.* The outer surface shows a gentle indentation for the acetabular border. As in early tetrapods generally the upper margin of the posterior projection of the bone is somewhat thickened. The area of the ischiadic symphysis is striated in a fashion seen in various early tetrapods.

No pubis is present in the material. Whether this is due to chance, or whether (particularly taking into account the immaturity of the specimen) the pubes were unossified, is, of course, uncertain.

Except for three phalanges or metapodials no identifiable remains of the hind leg are present.

DISCUSSION

Despite the fact that the remains are incomplete, the nature of *Proterogyrinus* seems clear as regards most features. The form is clearly an anthracosaurian; further, in most regards it is in close agreement with the Embolomeri of the Pennsylvanian and early Permian. Such portions of the skull as are preserved show a close approach to the structure seen in such representative Upper Carboniferous forms as *Pteroplax, Eogyrinus,* and *Palaeogyrinus* of the English Coal Measures (Watson, 1926; Panchen, 1964), *Neopteroplax* of the American Pennsylvanian (Romer, 1963), and, except in a lesser elongation of the snout, *Archeria* of the early Permian.[1] Even in the nature of the marginal teeth—small, numerous, closely crowded and with "chisel-like" tips—there is a clear comparison with embolomeres far removed in time, such as *Archeria* of the Permian. The humerus (except in the fact that ossification is less advanced) is closely comparable to that of such an embolomere as *Archeria.* The pelvis, too, is of a nature comparable to that of known embolomeres.

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[1] Figures of the roof of the *Archeria* skull (as *"Cricotus"*) have been given by Cope (1884), by Cope and Matthew (1915), and by Broom (1913). I hope to give a more complete description of *Archeria* cranial anatomy in the near future.

Were it not for the structure of the central region of the vertebrae, *Proterogyrinus* could well be considered a proper member of the Embolomeri, hardly to be distinguished on a family basis from various other members of that group. The central elements, however, give one pause. All previously known embolomeres in which vertebral material is present show both intercentra and pleurocentra as complete rings, as well ossified dorsally as laterally and ventrally, and with a thickness of ossification that reduces the opening for the notochord to a fairly modest diameter. In the present specimen the walls are relatively thin; most especially, both intercentrum and centrum are incomplete dorsally, with a broad gap in the region which in life lay below the neural canal. It must be kept in mind that the present specimen is rather certainly immature, and hence in an older specimen there may have been some degree of ossification in this area, in which, presumably, cartilage was already present. It is, however, rather certain that maturity would not have brought this area to the highly ossified condition seen in typical Embolomeri. This condition of the vertebrae has led me to erect for this form the new family Proterogyrinidae.

It is possible that the Proterogyrinidae represents a generalized type of anthracosaur, rather than a primitive group of embolomeres or embolomere ancestors. But because of the similarity in most features the Proterogyrinidae may, provisionally at least, be included in the Embolomeri.

The finding of this form, however, suggests reconsideration of generally accepted ideas of vertebral evolution in labyrinthodonts. A first major attempt at sorting out the membership of this group was that of Watson in his classic papers on the origin and evolution of the Amphibia (1919, 1926), in which he distinguished between the Rhachitomi, the Stereospondyli descended from them, and the Embolomeri. He considered the embolomeres to be the basal group of the entire Labyrinthodontia. In later years it became apparent that the story was somewhat different, and I proposed (Romer, 1947) that, leaving out of consideration the Devonian ichthyostegids, all labyrinthodonts could be divided into two major groups, Temnospondyli (including Rhachitomi and Stereospondyli) and Anthracosauria (including the Embolomeri and forms leading toward and to the Reptilia). This proposal assumed that in ancestral forms there was a large single intercentrum, centered ventrally, and

small paired pleurocentra, dorsolateral in position; that in the temnospondyls the pleurocentra remained small, and disappeared in stereospondyls, while in the Anthracosauria the pleurocentra enlarged to form the major central structure;[1] the embolomeres, as a side branch of the anthracosaurs, formed a variant in which intercentrum as well as pleurocentrum grew to form a second complete ring.

Since the publication of this thesis, nearly all more recent discoveries have tended to support it, although some variants in the temnospondyl pattern have been discovered, such as the peculiar plagiosaur group (Panchen, 1959) and *Doleserpeton* (Bolt, 1969). The nature of the centra in ichthyostegids (Jarvik, 1952) demonstrated the high antiquity of the temnospondyl pattern. My belief that the rhachitomous type was present at an early date has been confirmed by the finding by Baird (1957) that the loxommids, which had appeared before the close of the Mississippian, were rhachitomes, and by the discovery of typical rhachitomes in the Mississippian Greer quarry, including not only the specimen I have already described (Romer, 1969) but also others awaiting description.

In 1964 I elaborated further on a probable evolutionary pattern among anthracosaurs. I assumed that, beginning with the temnospondyl type of centrum, the pleurocentra grew downward, first in the form of two half rings,[2] and then consolidated into a complete ring, while the intercentra remained ventral wedges. I termed this the diplomerous condition. At this stage of phylogenetic development, I believed, there occurred a dichotomy, the embolomeres splitting off and developing the intercentra as well as pleurocentra

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[1] I consider here only the history of ossifications; as Panchen has pointed out (1963), either intercentrum or pleurocentrum, if it tends to take over the entire "central" area, includes in its substance the entire skeletogenous material of the segment, earlier split between the two types of element.

[2] A situation seen in *Pholidogaster*, which I interpreted as a primitive anthracosaur. Panchen (*in litteris*, and cf. Carroll, 1969) has disputed this, suggesting that *Pholidogaster* is a temnospondyl. The skull of the *Pholidogaster* type is too crushed to be interpretable, and Panchen believes that the anthracosaur skull in the Edinburgh collections which Watson and I thought to belong to this genus can not so be assigned. My belief in the anthracosaurian nature of this Lower Carboniferous form, however, was based mainly on the nature of the pleurocentra, which form two half-rings reaching the ventral surface of the column. Just this type of structure is seen in the immature specimens of the anthracosaur *Discosauriscus* (Spinar, 1953); temnospondyl pleurocentra are typically confined to a dorsal position, without ventral expansion.

into complete rings, while in the "main line" tending toward and to the reptilian condition (Seymouriamorpha in a broad sense), the intercentra failed to develop further and tended to be reduced.

Despite the restricted amount of material and its disassociated condition, the apparent nature of the *Proterogyrinus* column indicates that the story of anthracosaurian vertebral evolution needs reconsideration. In nearly every feature that can be made out in this new form, we are dealing with an animal closely allied to the embolomeres and perhaps to be included in that group in a broad sense. But, in conflict with my earlier beliefs, the pleurocentrum is not yet a complete ring, while the intercentrum is in an equally advanced condition. This suggests that the embolomeres split off from the anthracosaur "main line" at an earlier stage than I had thought was the case. Very probably further Mississippian discoveries at Greer and elsewhere will show that anthracosaur evolution was far more complex than I had assumed.

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